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ROLE OF NEST MICROCLIMATE AND FOOD AVAILABILITY IN CHICK DEVELOPMENT AND REPRODUCTIVE SUCCESS IN BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*)

by

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A Thesis Submitted to the Honors Council

For Honors in Animal Behavior

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ACKNOWLEDGEMENTS:

Collaborators

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All research was conducted under necessary state, federal, and institutional care permits, including approval through the Institutional Animal Care and Use Committee (IACUC) in the United States, the University Animal Care Committee (UACC) through McGill University in Canada, and proper permitting from the US Fish and Wildlife Service.

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ABSTRACT:

Seabirds are marine top predators, and as such are often studied as bioindicators of climate shifts (Oswald and Arnold 2012). Though many studies have analyzed the effect of macroclimatic variation on marine prey species availability and thus seabirds, few have analyzed effects of microclimate - fine spatial patterns of climate (Mantua and Hare 2002; Hatch 2013; Kim and Monaghan 2005a). I tested the hypothesis that localized temperature and humidity at nest sites interact with food availability to alter black-legged kittiwake (*Rissa tridactyla*) nest site quality, chick body condition during growth and development, and reproductive parameters including Julian lay date, number of eggs laid, and the proportion of chicks fledged per nest.

All black-legged kittiwakes were located in physically accessible nests along the exterior of an abandoned radar tower that now serves as a converted seabird laboratory. Nests were located on "panels" with distinct compass orientation, insolation, and exposure to wind and rain along the exterior of this polyhedral radar tower. Panels housed ~27 nests, alternating between supplementally fed (n = 4; all nests offered ad libitum food 3x/day) and unfed panels (n = 3). The supplemental feeding status of each nest remained unchanged for the duration of the dataset with the exception of panel G, which had supplemental food removed in the latter third of the breeding/chick rearing season. I recorded temperature and humidity at individual nest sites during egg laying and chick rearing (May-August 2017) on Middleton Island, AK using rainproof wireless sensor tags (Cao Gadgets, LLC). Measurements of chick developmental morphology (weight, wing, tarsus, culmen, headbill) were collected every five days. Nest site quality

was determined by analyzing the number of chicks fledged at individual nests over several years, therefore providing an historic analysis as well.

Microclimate varied across the tower, with warmest and driest panels being panels A through C and cooler more humid panels being panels D through G. Humidity and temperature were inversely related. Nests at fed panels maintained higher average temperatures and greater nest site quality than adjacent unfed panels. Microclimate minimally influenced egg laying of breeding adults and body condition of chicks. Warmer and drier nests tended to maintain earlier Julian lay dates and greater quantities of eggs laid. While food availability had a greater impact on growth and reproductive success, the data suggest that microclimate, specifically temperature and humidity, does explain some amount of variation in reproductive success.

I. INTRODUCTION:

This study focuses on the effect of nest microclimate and food availability on chick development and reproductive success in black-legged kittiwakes (*Rissa tridactyla*). Black-legged kittiwakes, or BLKI, are long-lived seabirds with lifespans of up to 25 to 30 years. The longevity of BLKI allows individuals to be reproductively active over many years, potentially selecting for them to adjust their breeding parameters and reproductive investment from one year to the next in response to environmental fluctuations (Kitaysky, Wingfield, and Piatt 2001; Maunder and Threlfall 1972). What is really interesting about these birds, and what makes them particularly relevant to the present study, is that they are often recognized as marine bioindicator species.

The Black-Legged Kittiwake: A Marine Bioindicator

A marine bioindicator species is an organism that has some aspect of its life history tied to changes in the marine ecosystem. In the case of BLKI this life history trait is reproductive success. Based on criteria set forth by Oswald and Arnold (2012), the criteria for marine bioindicators is as follows: "medium-distance or long-distance migrations, thermally exposed breeding sites, strong dependence on marine prey, and well documented thermoregulatory adaptations and behaviors." As our climate continues to change, bioindicator species will become increasingly more relevant study subjects in the process of determining how these changes are affecting ecosystems and trophic webs throughout the globe. BLKI meet these criteria as migratory cliff-nesting subarctic seabirds, with their reproductive success often being tightly related to fluctuations in the marine ecosystem. Therefore, BLKI are an excellent species to study in relation to

different levels of climate and its impacts on reproductive success, especially in the context of the present study in which I test the hypothesis that fine scale patterns of climate at the nest site, known as nest site microclimate, have an effect on BLKI reproduction and chick development. The qualification of BLKI as marine bioindicators also lends them to be particularly useful in determining the magnitude to which our rapidly changing climate is affecting environmentally sensitive species (IPCC 2007).

The colony of BLKI I worked with was located on Middleton Island, Alaska, which sits in the Gulf of Alaska along a continental shelf. The continental shelf creates upwellings that provide nutrients for a variety of marine life such as phytoplankton, which then support an abundance of marine prey species further up in the trophic web such as BLKI's main food source, the fish species capelin (*Mallotus villosus*) (Barth et al. 2007). However, marine prey species abundance fluctuates quite notably. This fluctuation and its effects over the last roughly thirty years has been monitored through long-term monitoring studies conducted on Middleton Island (Hatch 2013; ISRC 2016; ISRC 2017). The research station on Middleton Island is both the site of a long-term BLKI monitoring study, which began upon the site's inception in 1982, as well as the site of a food-manipulation study. The long-term monitoring study allows scientists to quantify how reproductive success fluctuates from year to year (Figure 1), particularly in relation to shifts in the marine ecosystem. The food-manipulation study on Middleton Island allows scientists to remove limitations on food availability for some of these birds, which helps assesses the effects of interannual variation in naturally available food resources (that result from shifts in climate) on BLKIs' reproductive success.

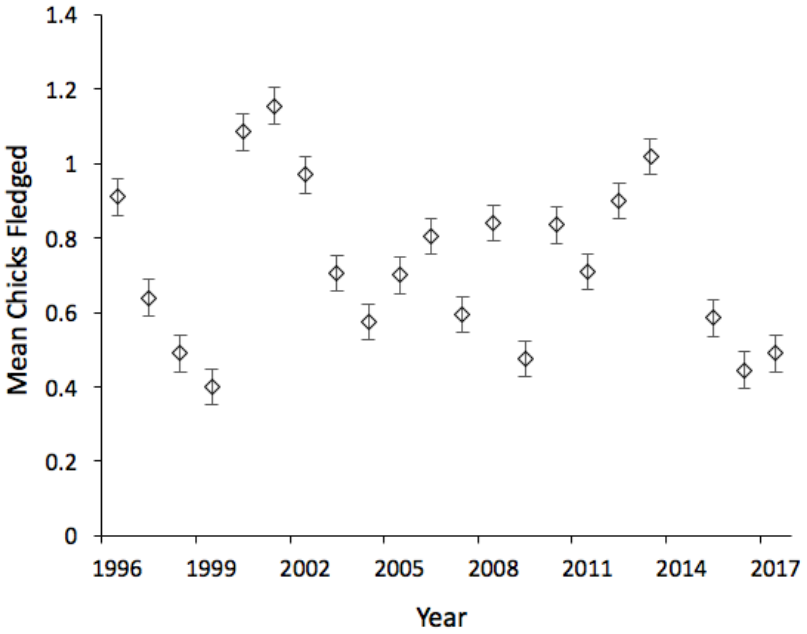


Figure 1. Reproductive success, quantified by mean chicks fledged per nest, of monitored BLKI nesting on Middleton Island from 1996-2017; Bars = standard error (SE)

Macroclimate: The Pacific Decadal Oscillation and Food Availability

The shifts in the marine ecosystem that affect natural food availability for these birds are driven primarily by macroclimate, or large scale global and/or regional patterns of climate. The Pacific Decadal Oscillation, or PDO, is a climate index that reflects changes in sea surface temperature (SST) between warm and cool SST phases (Figure 2). Such changes in SST lead to variation of the types and quantities of marine prey species present during a given season, with BLKI's main food source capelin found in abundance during relatively cooler SST phases, while less desirable and nutritionally beneficial species for BLKI such as crustaceans and mollusks and more readily available during relatively warmer SST phases (Mantua and Hare 2002; Hatch 2013). Capelin are often far sparser during periods of warmer SST. These changes in the types and quantities of marine prey species available during any given breeding season are often reflected in

BLKIs' reproductive success as top marine predators, ultimately suggesting that macroclimate influences food availability by shifting trophic interactions at a lower level within the food chain, which then influences at least a portion of variation in the reproductive success of BLKI (Frederiksen, Harris, Daunt, Rothery, and Wanless 2004; Hatch 2013; Grémillet and Boulinier 2009).

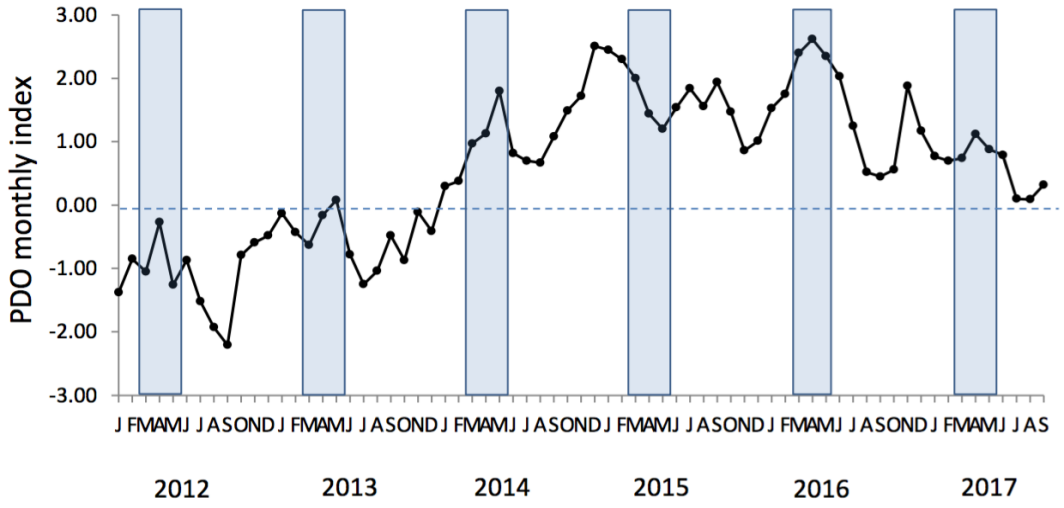


Figure 2. PDO monthly index indicating general trends of SST over the past five years. Months are indicated with a single letter. The shaded bars indicate the period just prior to the breeding season (March through May, with breeding season May through August), which determines marine prey species availability for a given breeding season. Figure obtained from ISRC (2017).

There has been a warming trend in the PDO for about the past five years (Figure 2). PDO monthly indices are correlated with SST and consequently whether or not that year was a "good" or "bad" year for BLKI based on which marine prey species the SST suited. A negative PDO monthly index indicates cooler SST and therefore greater presence of cold water fish species, primarily capelin, and ultimately a better year for

BLKI. A positive PDO monthly index, however, indicates warmer SST and therefore decreased presence of fish. Consequently, BLKI will consume far more crustaceans and mollusks (lower-quality prey in terms of energy content) out of necessity and travel further distances to forage for food (ISRC 2017).

The food manipulation study conducted on Middleton Island functionally removes the influence of macroclimate on food availability for half the birds involved in this study by providing unlimited food supplementation of capelin during the breeding season. This study separates birds into "fed" and "unfed" conditions, with fed birds receiving capelin ad libitum, or until they refuse further food, three times a day at 0900, 1300, and 1800 hours. In the fed condition, adult birds are fed whole capelin and frequently consume anywhere between zero and eight fish (approximately 30 grams per fish) in a single feeding. Feeding begins in the pre-laying period when the birds arrive on the island in early May and continues throughout the breeding season until the chicks fledge in mid-August. The remaining unfed birds rely solely on naturally available food sources, with all birds (both fed and unfed alike) maintaining free access to foraging at sea (Gill and Hatch 2002).

Study Site – Middleton Island, Alaska

The research site on Middleton Island lends itself well to both the long-term monitoring study as well as the food manipulation study because the BLKI at this site nest on what was once an abandoned military radar tower. Middleton Island was used as a military base during the Cold War but was then abandoned in 1963. Once the military left the site all that remained were the empty, crumbling office, dormitory, and air force

operation buildings and radar towers. One of these structures was a particularly large radar tower, roughly 60 feet in height (Gill and Hatch 2002). The tower was put back into use upon its conversion to a functional seabird laboratory and nesting site by Dr. Scott Hatch with the Institute for Seabird Research and Conservation (the ISRC; a non-governmental research organization) in 1982 – an idea that came to fruition upon his visit to the island during which he noticed BLKI haphazardly nesting along the tower's deteriorating structure. The tower provided such an excellent nesting site for many of these birds because BLKI are naturally colonial cliff nesters, and as such they typically build their nests along elevated, exposed faces such as rocky cliffs along the ocean's edge. Being a similarly elevated and exposed space, the tower provided an excellent man-made "cliff" alternative.

Due to modifications made by Dr. Hatch, the tower now provides a structure for scientists to closely observe and even handle these free-living nesting BLKI. Field crews that arrive on the island each year monitor stages of breeding, egg laying, chick rearing, and fledging for BLKI that nest on and around the tower. Scott Hatch and the ISRC have overseen this operation each year, and many collaborators arrive at the island throughout the season as well to conduct their own independent experiments in addition to the yearly data collection on the productivity of the colony. The intensive BLKI research at Middleton is possible because the tower is a polyhedral structure broken into panels, which are individual faces around the outside of the tower (Figure 3). Each panel contains three rows of roughly nine nests each, resulting in a total of around 27 nests per panel. The panels of focus for the present study are panels A through G. Each individual

nest on these panels is directly accessible from the inside of the tower through sliding one-way mirrored glass. These allow for direct access to nesting adults, eggs, and chicks at each individual nest site when necessary, but they also allow for behavioral observations of these birds in the nest without disturbing them (Gill and Hatch 2002). The fed and unfed conditions within the food supplementation study alternate across these panels, with panel A being a fed panel in which nearly all nests on that panel receive food supplementation through a tube placed on one side of the nest, and panel B being an unfed panel in which all nests on that panel do not receive food supplementation. As many as three nests within a given fed panel were not fed because the width of certain nest sites was simply too small to fit a feeding tube alongside the nest. This alternation in feeding conditions continued around the tower, with Panel C being fed and panel D being unfed, and so on through panel F. G panel was unusual, in that it was fed for the first part of the season, but feeding was halted during chick rearing.

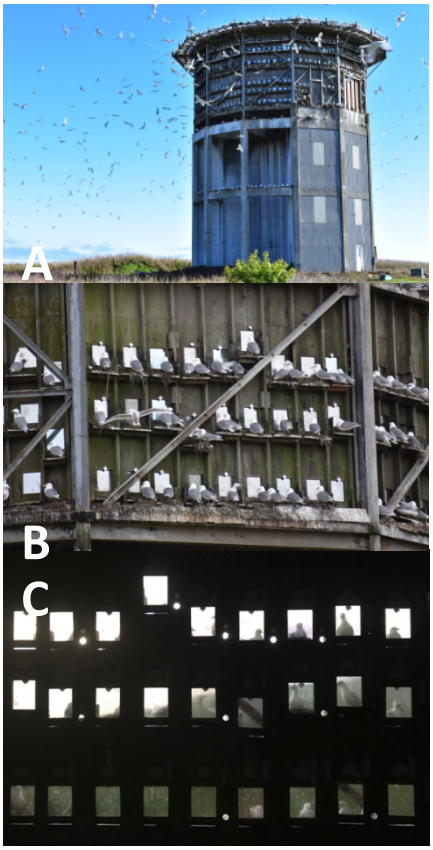


Figure 3. A. Full tower; B. View of a single panel from the outside; C. View of a single panel from the inside (looking through sliding one way mirrors out into nesting sites)

Prior studies have consistently demonstrated that food availability, driven by fluctuations in macroclimate, affects clutch size (number of eggs laid in the brood of a

nesting pair), Julian lay date (number associated with the date on which an egg was laid; January 1 = day 0, December 31 = day 365), chick growth/development (quantified via calculations of chick body condition indices based on morphometric measurements), and fledging success (number of chicks that successfully left the nest) of BLKI breeding on Middleton Island (Gill and Hatch 2002). Food supplementation bolstered each of these parameters, leading to larger clutch sizes, increased fledging success, and greater overall productivity, which has been demonstrated through analyses of historic data collected at Middleton Island (Gill and Hatch 2002; Gill, Hatch, and Lanctot 2002).

The food supplementation study allows us to essentially decouple the effects of macroclimate on fed birds by eliminating natural fluctuations in a food resource. Based on our understanding of macroclimate and its effect on food availability, I would expect food availability to be one of the primary drivers of reproductive success. Therefore, by providing consistent food supplementation to fed nests, I would expect to see very little variation in these fed nests' reproductive success. However, though the reproductive success of fed birds is typically higher than that of unfed birds, fed birds still exhibit interannual fluctuations in reproductive success that tend to track the rise and fall in reproductive success seen in unfed birds (Figure 4). Such patterns suggest that food availability during the breeding season is not the sole driver of variation in reproductive success, and that other variables may contributing to reproductive variation.

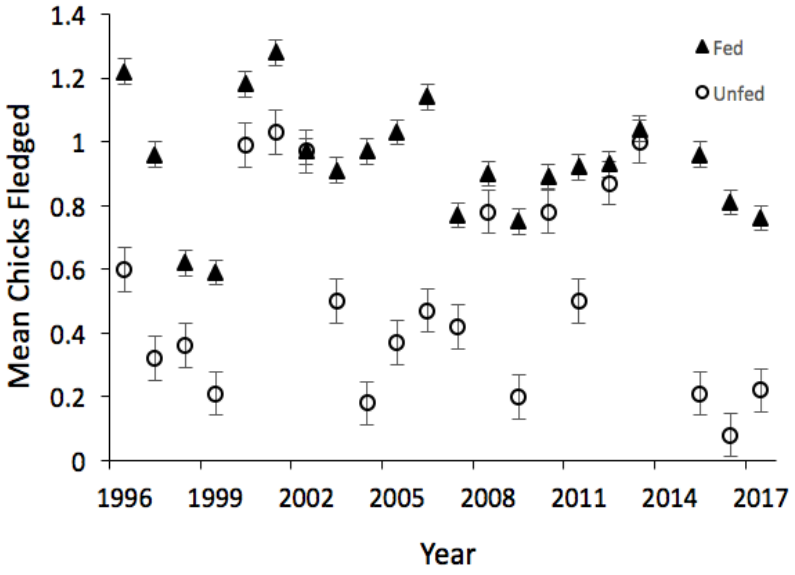


Figure 4. Reproductive success, quantified by mean chicks fledged per year, of BLKI nesting on the Middleton tower from 1996-2017 separated into fed and unfed conditions; Bars = SE

Research Question and Hypothesis

Ultimately, even though supplemental feeding improves reproductive success, it still does not account for all variation in reproductive success (Figure 4). This brought me to my research question: what explains variation in reproductive parameters in these food-supplemented nests? I hypothesized that nest microclimate, or the fine spatial patterns of weather (particularly temperature and humidity) at the nest site level, contributes to variation not explained by food availability within a given breeding season. I chose to test this hypothesis due to my interest in the effects of our changing climate at a variety of spatial levels, from local to global, on ecosystem functions. I am particularly interested in how climate change can affect marine ecosystems, particularly top marine predators such as BLKI, which are also migratory birds and therefore experience a variety of local and/or regional climates throughout their migratory paths. As a result, I

wondered if kittiwakes would demonstrate any sensitivity to smaller scale climate, or microclimate, at their breeding site, which has the potential to differ quite notably and unpredictably from many of the other microclimates they experience outside of the breeding season.

Studies have shown that microclimate affects aspects of reproduction and chick growth and development among a variety of seabird and wetland bird species, including lesser black-backed gulls (*Larus fuscus*), purple swamphens (*porphyria porphyria*), lesser whistling ducks (*Dendrocygna javanica*), and pink-necked green pigeons (*Treron vernans*) (Kim and Monaghan 2005a; Rajpar and Zakaria 2011). Kim and Monaghan (2005a) found that ground nesting lesser black-backed gulls preferentially select nest sites based on vegetation height for protection from predators and a more stable microclimate to maintain constant temperature regimes for incubation. Rajpar and Zakaria (2011) determined that nest microclimate is one of three key characteristics that determined the distribution, density, and diversity of the wetland bird species listed above. They write that these three key characteristics are as follows:

> Vegetation composition (i.e. emergent and submerged vegetations, grasses, shrubs, and trees), vegetation structures (tree diameter and height), and microclimate variables (temperature, relative humidity and light intensity) (Rajpar and Zakaria 2011)

Since BLKI are cliff nesters, the vegetation component of this system is not as relevant, and so I chose to focus specifically on the characteristics of microclimate.

In addition to evidence indicating an effect of microclimate on several ground-nesting bird species, records of field observations at Middleton Island suggest that microclimate may impact BLKI in exposed nests, with observations of both adults and chicks in direct sunlight exhibiting gaping behavior. Gaping behavior is a form of behavioral thermoregulation similar to panting performed by birds in order to maintain a stable core body temperature. Thermoregulatory behaviors are usually associated with energetic costs, which may be reflected in adults' reproductive success or chicks' growth and development. Thus, in this project I explored the role of variation in nest microclimate on a cliff-nesting seabird species that inhabits thermally exposed nest sites on the sides of cliffs, or in this case the side of a radar tower.

Predictions

My hypothesis that nest microclimate contributes to variation in reproductive parameters and chick growth and development within a given breeding season generates several predictions. I predict that nest microclimate will affect Julian lay date and clutch size. This prediction is based on literature that indicates Julian lay date and clutch size can be influenced by variables to which breeding individuals are exposed for only a short period of time upon arriving at the breeding site, including food availability at the breeding site (Klomp, 1970; Gill, Hatch, & Lanctot 2002). Therefore, it is also possible that short-term exposure to nest site microclimate during the nest building and pre-laying period may influence these variables. Additionally, Frederiksen et al. (2004) suggested that if BLKI, which maintain widespread migration patterns and therefore often sense climatic shifts at a very large environmental scale (that of macroclimate), are unable to

change the scale at which they process and respond to environmental variation, they may be very heavily impacted by climate change. However, they also suggested that BLKI may be able to sense the smaller scale environmental cues of their breeding site (microclimate) very soon upon arrival, and may be able to adjust the timing of their breeding and reproductive parameters accordingly. Therefore, if BLKI on Middleton Island maintain the ability to adjust their reproductive parameters to microclimate at the breeding site, I would expect to see a relationship between these reproductive parameters (particularly the timing of egg laying known as Julian lay date) and nest temperature and humidity.

I also predict that nest microclimate will affect chick growth and development and fledging success, based on results by Kim and Monaghan (2005a) and Rajpar and Zakaria (2011). Though Kim and Monaghan (2005a) determined that chick growth was not affected by nest site vegetation and microclimate in the ground-nesting lesser black-backed gulls, I wanted to explore if chick growth would be affected in a thermally exposed cliff-nesting species. This prediction is also rooted in the body of literature on thermoregulation and the behavioral, physiological, and ultimately energetic costs associated with endotherms expending energy to regulate their body temperature in a variety of environmental conditions (Boyles, Seebacher, Smit, and McKechnie 2011). I would expect the costs and benefits of thermoregulation to be most relevant in the context of chicks during their growth and development up through fledging based on age differences in chicks' abilities to thermoregulate found in other bird species. Several studies have indicated that young birds are most sensitive to their surrounding climate

before they have developed the ability to successfully thermoregulate (Tortosa and Villafuerte 1999; Lasiewski and Snyder 1969; Pedersen and Steen 1979).

Finally, if nest site microclimate were to have a strong effect on overall reproductive success at a specific nesting site, I would expect to see this effect apparent in the relationship between microclimate and long-term reproductive success at a given site. The variable "nest site quality" (or Q) summarizes several years' worth of reproduction at a given nest site as the total number of chicks fledged at a nest site between the years 2000 and 2017 divided by the total number of years that nest was occupied (Kokko, Harris, and Wanless 2004). Q therefore aids in determining if spatial variation in microclimate (based on variation in the location and orientation of individual nests) imposes an effect on reproduction over several years. It is important to note that Q focuses on the reproductive success of a variety of individuals that occupied any single nest site over several years, rather than following the yearly reproductive success of a specific pair of individuals who may inhabit different nest sites each year.

II. MATERIALS AND METHODS:

Reproductive Parameters and Chick Growth and Development

In order to test my hypothesis, I collected data on reproductive parameters, chick growth and development, and microclimate throughout the 2017 BLKI breeding season (May through August). Among the reproductive parameters monitored for each nest were Julian lay date (the number associated with the date on which an egg was laid, for example January 1 = day 1 and December 31 = day 365), the number of eggs laid,

number of eggs hatched, and the number of chicks fledged. Chick mass and body measurements were recorded every five days. The chick body measurement of focus for the present study was wing length, which grew most linearly over time ($r^2 = 0.953$) among all measurements taken (wing length, tarsus length (length of bone in lower leg), culmen length (length of bill), and headbill length (length from the back of the head to the tip of the bill)).

Microclimate Monitoring

Microclimate was measured from May through August 2017 using 20 Rainproof Wireless Sensor Tags (Cao Gadgets, LLC) (Figure 5). Temperature and humidity were recorded simultaneously on intervals ranging between 5 and 30 minutes. These sensors were hung at individual nest sites roughly 5 centimeters above the sliding one-way glass mirrors at each nest (~30 cm above the base of the nest).

Figure 5. Weather proof microclimate sensors (Rainproof Wireless Sensor Tags) from Cao Gadgets, LLC (dimensions: 41 x 41 x 8.5 mm)

Microclimate was measured via two different methods: 1. Simultaneous monitoring of panels A through G and 2. Individual panel "mapping." Simultaneous panel monitoring involved deploying all 20 sensors across all seven panels, A through G, with roughly three sensors on each panel. Simultaneous panel monitoring was done throughout a majority of egg laying and chick rearing (between June 16, 2017 and August 14, 2017 when microclimate mapping was not occurring due to limitations of

sensor availability). Simultaneous monitoring of all panels provided representative microclimate readings for each panel concurrently, which allowed me to directly compare measurements from each panel and therefore characterize general microclimate of each panel (expected to differ based on compass orientation, and therefore insolation and wind patterns) relative to the others.

Individual panel "mapping," however, was done for one panel at a time. During panel "mapping," which occurred twice during the season for each panel, all 20 sensors were deployed at once on twenty random nests within a single panel, which contains roughly 27 nests in total. All twenty sensors were deployed on each panel for 24 hours on a qualitatively sunny and warmer day as well as 24 hours on a cloudy, cooler day. The microclimate mapping data set does not allow for direct comparisons of microclimate between panels because each panel was mapped on a separate day, however it does provide the ability to directly compare nests within each panel and therefore determine if there are any fine spatial patterns of microclimatic variation within a given panel. This finer scale of resolution within each panel allowed me to look at the spatial patterns of climate within each panel in relation to records of reproductive success and chick growth and development at each nest site.

In order to easily visualize spatial variation in microclimate between nests within a given panel using microclimate mapping data, individual temperature and humidity readings were ranked for use in qualitative observations of within panel variation between nests in panels A through G (1 = lowest measurement, N = highest measurement). These ranks were only used to visually explore spatial patterns in

microclimate measurements since raw measurements were not directly comparable across panels due to the collection of microclimate data for each panel on different days. Raw measurements (as opposed to ranked) of temperature and humidity were used in all statistical analyses.

Microclimate Sensor Validation

I quantified inter-sensor variation in order to validate microclimate sensor readings. I exposed 9 sensors to the same temperature and humidity regimes simultaneously and then quantified the variation in each sensor's readings by conducting five random pairwise comparisons of sensors, all on measurements collected in the same 60-minute interval, to obtain the coefficient of variation (CV) for each sensor pair. The mean CV for sensor validation comparisons was 1.77% +/- 0.94 for temperature measurements and 1.46% +/- 1.67 for humidity measurements. This is lower than CVs calculated for comparisons of data collected from different sensors simultaneously in the field, with mean CV for nest temperature measurements being 6.75% +/- 4.41 and mean CV for nest humidity measurements being 5.41% +/- 3.82. These results confirm that variation in microclimate measurements among nests and panels was greater than variation among sensors.

Dependent Variables

Among the parameters of reproduction and chick growth and development that were monitored during the 2017 breeding season, Julian lay date, clutch size (the number of eggs laid in the brood of a nesting pair), chick body condition index ("BCI"; residual values from regressing body mass against wing length based on Schulte-Hostedde,

Zinner, Millar, and Hickling (2005)), and the proportion of chicks fledged ("PCF"; the number of chicks that successfully left the nest divided by the number of eggs hatched per nest) were all analyzed statistically. Chick BCI essentially quantifies how heavy a chick is in relation to its structural size. Assessing BCI can serve as a proxy for the energetic reserves of chicks, and ultimately reflects parental investment. Chick BCI was calculated for chicks at age 30 days, which is toward the end of their nestling period. Julian lay date and clutch size are important in quantifying whether birds at certain nest sites are affected by microclimate during the egg laying stage of breeding, whereas chick body condition index (BCI) and the proportion of chicks fledged (PCF) provide a representative metric of breeding adult success in caring and providing for chicks during the chick rearing period, as well as chicks' resilience (or lack thereof) to climatic exposure in the nest.

An additional variable —nest site quality—was an historic variable in that it captured reproductive success at a given nest site over several years. Nest site quality (Q) was calculated as the total number of chicks fledged at a nest site between 2000 and 2017 divided by the total number of years that nest was occupied (Kokko, Harris, and Wanless 2004). Assessing historic reproductive success is important because it controls for any notable variation in reproductive success due to a specific year's effects. For example, there could be an independent event, such as an oil spill, that occurs in the span of a single breeding season that dramatically impacts marine prey species availability. This event could lead to more dramatic variation in reproductive success during that season than a breeding season during a different, more "stable" year. The averaging of

reproductive success over several years therefore controls for these kinds of potential year effects. As a result, Q provides a holistic representation of reproductive success at a given nest site over time.

Q is also important because if we see an effect of microclimate on variables measured only during the 2017 season, those results could be driven by phenomena specific to that year. We assumed microclimate would be relatively constant between nests each year. Therefore, if we see an effect of microclimate on a metric of historic reproductive success summarized over several years we can more firmly conclude that microclimate does in fact influence reproductive success and that any quantifiable effects of microclimate are not simply characteristic to any one breeding season alone.

Given the overall hypothesis and associated predictions, these data were then used to answer the following questions: 1. Is there significant variation in microclimate between panels along the tower? 2. Is there significant variation in microclimate between individual nests within a given panel? 3. How does microclimate affect reproductive parameters and chick growth during the 2017 breeding season at both the panel wide and nest site specific level? 4. Is there any effect of microclimate on reproductive success at individual nest sites over time?

Statistical Analysis

The statistical analyses used to explore these questions were conducted in JMP and SPSS statistical software. All one-way ANOVAs and Pearson correlations were conducted in JMP Pro 11 (Version 11.1.1), and one-way ANCOVAs were conducted in SPSS (Version 24). All tests are summarized in Table 1. In order to characterize how

microclimate varied between panels across the tower, daily means of temperature and humidity data obtained from sensors deployed simultaneously across all panels during the egg laying and chick rearing period (approximately 3 sensors per panel) were included in a one-way analysis of variance (ANOVA) with a Tukey-Kramer HSD post-hoc test between all panels (A through G). Variance in temperature and humidity were analyzed similarly in order to quantify variability in microclimate by determining how far each panel's microclimate measurements were from the mean values. The resulting Tukey-Kramer HSD post-hoc test provided direct pairwise comparisons between all panels.

I ran a Pearson correlation using microclimate mapping data between mean nest temperature on a sunny day and mean nest temperature on a cloudy day, as well as between mean nest humidity on a sunny day and mean nest humidity on a cloudy day. This correlation allowed me to determine if analyzing sunny and cloudy days separately was necessary, or if the two were so similar that analyzing one would capture variation observed in both.

In order to determine if there was significant variation in microclimate between nests within individual panels, one-way ANOVAs were conducted on raw temperature and humidity measurements for all nests within each panel, with seven panels in total and therefore seven total one-way ANOVAs per sunny/warm microclimate mapping condition and seven per cloudy/cool microclimate mapping condition. These one-way ANOVAs were run with nest site as the independent variable and temperature and humidity each as separate dependent variables.

Microclimate mapping was broken into sunny/warm condition and cloudy/cool condition because these sunny/warm days are likely to capture extremes of potential heat and humidity exposure compared to typical days at the study site, which are regularly cloudy/cool and relatively damp. Exposure to heat is expected to impact BLKI more than typical cloudy/cool weather would and therefore reveal more meaningful variation between nest sites based on nest location and exposure (Lasiewski and Snyder 1969; Boyles et al. 2011).

In order to analyze the effect of microclimate on reproductive success and chick growth and development at the scale of whole panels, one-way ANCOVAs were conducted with the fixed factor of fed/unfed condition and with mean temperature and mean humidity of panels A through F as covariates. Panel G was left out of analyses of microclimate's effect on reproduction and chick growth due to its initial supplemental feeding during the first part of the season but then removal of feeding during chick rearing, which likely affected the reproductive success of birds on that panel. Separate models were run for each dependent variable (Julian lay date, clutch size, chick BCI, PCF, and Q for each individual nest). Panel was not included as a fixed effect because the microclimate data used in these analyses were obtained from simultaneous panel microclimate monitoring for the duration of the breeding season (unlike with individual nest microclimate mapping, which occurred on separate days for each panel). Similar models were run again separately with the covariates of temperature variance and humidity variance for each panel to determine the effect of microclimatic variability on reproductive success and chick growth and development. These one-way ANCOVAs

explored the effect of microclimate at the panel level because I measured the microclimate of three sites from each panel simultaneously throughout the egg laying and chick rearing period, therefore allowing for direct panel to panel comparisons.

Due to the fact that microclimate mapping data was collected on separate days, conducting a similar model at the nest-site specific level required incorporating panel as a random effect which then controlled for any variation in measurements between panels due to the temporal separation in microclimate mapping measurements. As a result, models were run with the addition of panel as a random effect, with a separate model run for each dependent variable of Julian lay date, clutch size, chick BCI, PCF, and Q and nest site microclimatic variables (means and variances of temperature and humidity) as covariates. Separate models were run for microclimate means and microclimate variances obtained from microclimate mapping data on both sunny/warm days and cloudy/cool days.

Pearson correlations were then conducted between any independent and dependent variables that demonstrated significance in the one-way ANCOVA. These one-way ANCOVAs were used to test the following hypotheses: 1. Microclimate contributes to some variation in reproductive parameters, 2. There is an effect of microclimate on chick growth and development, and 3. Variation in microclimate helps explain variation in an historic representation of reproductive success at individual nest sites.

Table 1. Summary of all statistical analyses

Panel comparisons of microclimate:	Analysis of the effect of microclimate on average reproductive parameters and chick growth/development *per panel*	Analysis of the effect of microclimate on average reproductive parameters and chick growth/development *per nest*

• One-way ANOVA	• One-way ANCOVA
	  • Fixed Effect: Feeding condition
	  • Covariates: Temperature and humidity (mean and variance)
	  • Separate model run for each dependent variable:
	  • Julian lay date
	  • Clutch size
	  • Chick BCI
	  • PCF
	  • Q
		• One-way ANCOVA
		  • Random Effect: Panel
		  • Covariates: Temperature and humidity (mean and variance)
		  • Separate model run for each dependent variable:
		  • Julian lay date
		  • Clutch size
		  • Chick BCI
		  • PCF
		  • Q

III. RESULTS:

Simultaneous Panel Microclimate Monitoring

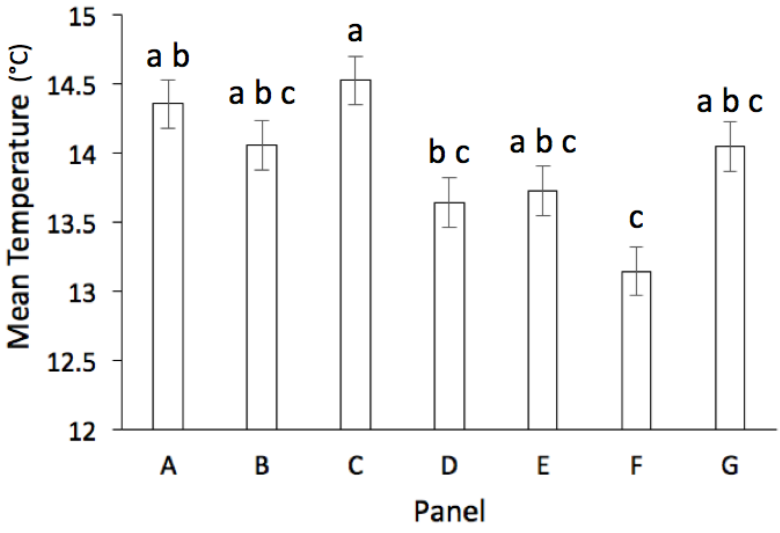
An ANOVA determined that there was significant variation in mean temperature between panels ($F(6, 746) = 4.4929$, $p = 0.0002$). A Tukey-Kramer HSD post-hoc analysis provided direct paired comparisons of all panels' mean temperatures during the egg laying and chick rearing season, which found significant differences in mean temperature between panels C and F, C and D, and A and F (Table 2).

Table 2. a.) ANOVA comparing mean temperature (°C) between panels during the egg laying and chick rearing period and b.) associated post hoc tests (connecting letters report); bars that share a lower case letter (placed above each bar) are not significantly different from each other ($p < 0.05$); bars = standard error (SE)

a. ANOVA Table:

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Panel	6	129.0656	21.5109	4.4929	0.0002*
Error	746	3571.6863	4.7878		
C. Total	752	3700.7519			

a. Post Hoc Test:



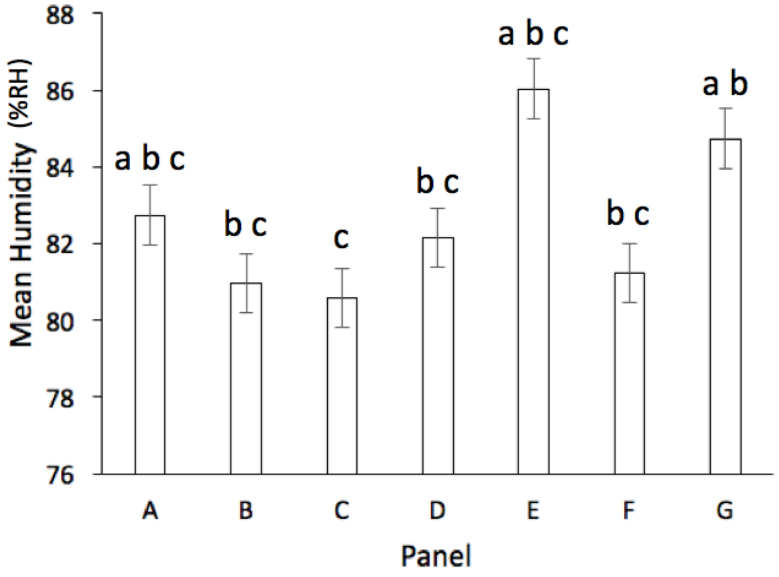
An ANOVA also revealed significant variation in mean humidity between panels ($F(6, 746) = 5.1963$, $p < 0.0001$). A Tukey-Kramer HSD post hoc analysis also indicated between which panels significant differences in mean humidity exist (Table 3).

Table 3. a.) ANOVA comparing mean humidity (%RH) between panels during the egg laying and chick rearing period and b.) associated post hoc tests (connecting letters report). Separate letters indicate significant differences between panels ($p <$ 0.05), providing direct panel to panel mean temperature comparisons. Bars = SE

a. ANOVA Table:

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Panel	6	2662.199	443.7	5.1963	< 0.0001*
Error	746	63699.782	85.388		
C. Total	752	66361.981			

b. Post Hoc Test:



Similarly, ANOVAs of temperature variance and humidity variance for each panel during the egg laying and chick rearing season found significant differences in temperature variance between panels ($F(6, 746) = 10.6544$, $p < 0.0001$) as well as in humidity variance between panels ($F(6, 746) = 9.9190$, $p < 0.0001$), therefore demonstrating that certain panels experience different degrees of microclimatic variability. Tukey-Kramer HSD post hoc analyses provided connecting letter reports

indicating the distinct differences between individual panels that do not share any overlapping lowercase letters listed above each panel's respective bar (Tables 4 & 5).

Table 4. a.) ANOVA comparing temperature variance (°C) between panels during the egg laying and chick rearing period and b.) associated post hoc tests (connecting letters report). Separate letters indicate significant differences between panels ($p < 0.05$), providing direct panel to panel mean temperature comparisons. Bars = SE

b. ANOVA Table:

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Panel	6	5208.150	868.025	10.6544	< 0.0001*
Error	746	60777.269	81.471		
C. Total	752	65985.419			

b. Post Hoc Test:

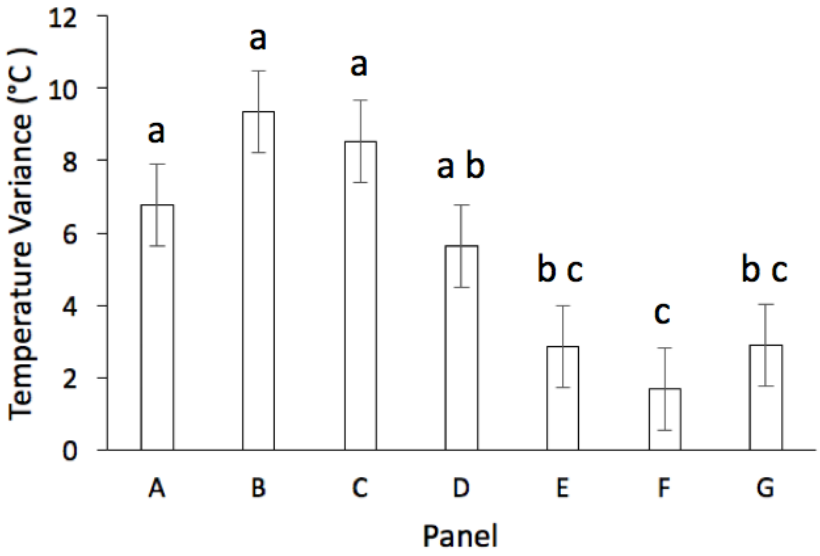
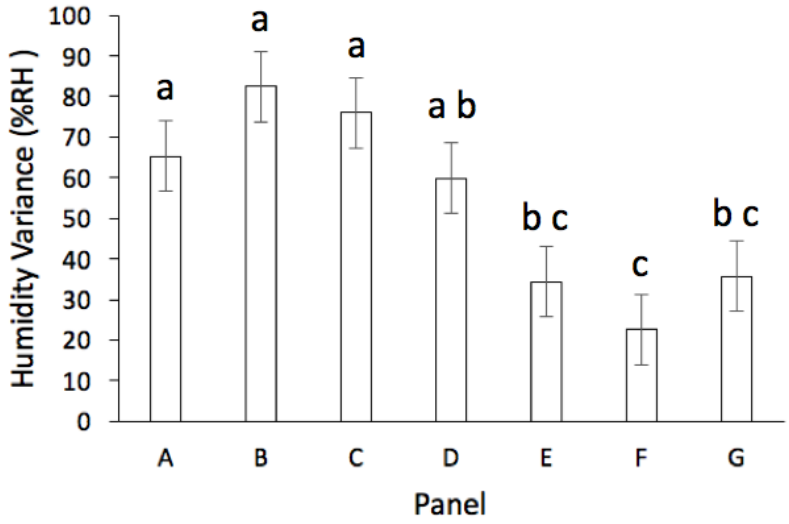


Table 5. a.) ANOVA comparing humidity variance (%RH) between panels during the egg laying and chick rearing period and b.) associated post hoc tests (connecting letters report). Separate letters indicate significant differences between panels ($p < 0.05$), providing direct panel to panel mean temperature comparisons. Bars = SE

a. ANOVA Table:

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Panel	6	303177.0	50529.5	9.9190	< 0.0001*
Error	746	3800265.6	5094.2		
C. Total	752	4103442.6			

b. Post Hoc Test:



Ultimately, panels A, B, and C maintained some of the highest mean temperatures and greatest variation in recorded temperatures, with mean temperatures and temperature variance generally greater than those of panels D, E, F, and G. Panels A, B, and C also maintained higher variance in humidity than panels D, E, F, and G, which was consistent with the more variable and extreme microclimatic exposure seen amongst panels A

through C. Consistent with the inverse relationship between temperature and humidity (Figure 6), the cooler panels on average – panels D, E, F, and G – generally maintained higher average humidity than panels A, B, and C. The seasonal minimum temperature across the entire tower was 7.19°C and the maximum temperature was 33.83°C. The seasonal minimum humidity was 22.08% RH and the maximum was 100% RH.

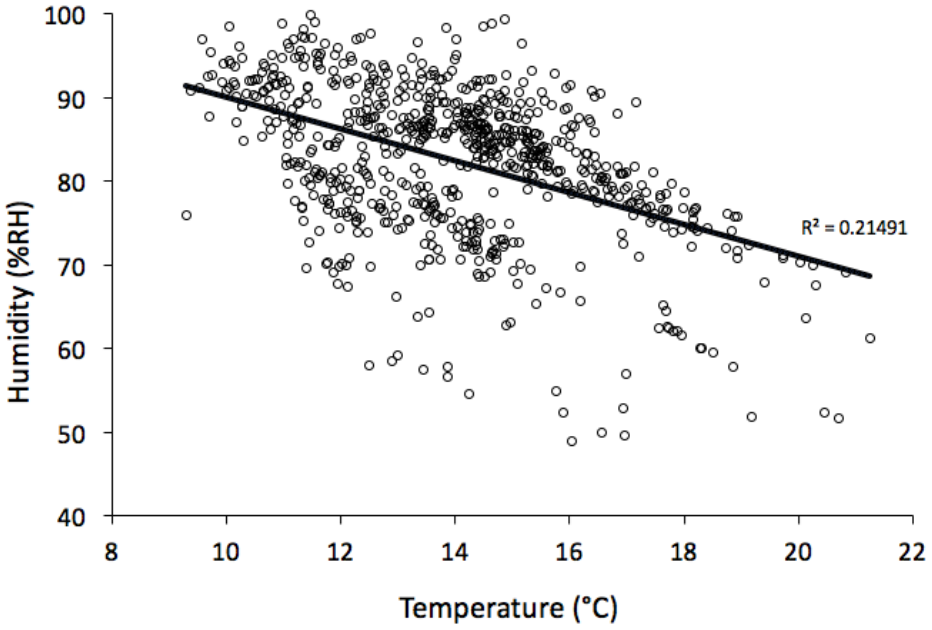


Figure 6. Inverse relationship between mean nest temperature (°C) and mean nest humidity (%RH) per day during egg laying and chick rearing

Microclimate Mapping

There was a significant positive correlation between sunny day mean temperature measurements (12.884°C +/- 1.561; all statistics reported as mean +/- standard deviation) and cloudy day mean temperature measurements (11.849°C +/- 1.976), $r = 0.37$, $p < 0.0001$, $n = 105$, indicating that mean temperature on qualitatively sunny/warm days and

mean temperature on qualitatively cloudy/cool days were related; however, there was still a lot of variation unexplained with a fit of only 0.37. There was no significant correlation, however, between sunny day mean humidity measurements (76.304% RH +/- 3.895) and cloudy day humidity measurements (84.682% RH +/- 4.218), $r = 0.03$, $p = 0.7471$, $n = 105$, indicating the two differ based on sunny and cloudy condition, with cloudy day humidity being higher than sunny day humidity. These results indicate that sunny day and cloudy day temperature and humidity readings should each be analyzed separately.

Sunny/Warm Day Mapping

Panels A, B, C, D, E, F, and G were mapped on separate days that were qualitatively determined in the field to be sunny, warm, and relatively clear days at the study site. Some variation was observed between nests within each of these 7 panels (Figure 7). However, not all panels showed significant variation among nests in mean temperature or mean humidity. There was more significant variation in humidity than temperature among most panels (Table 6).

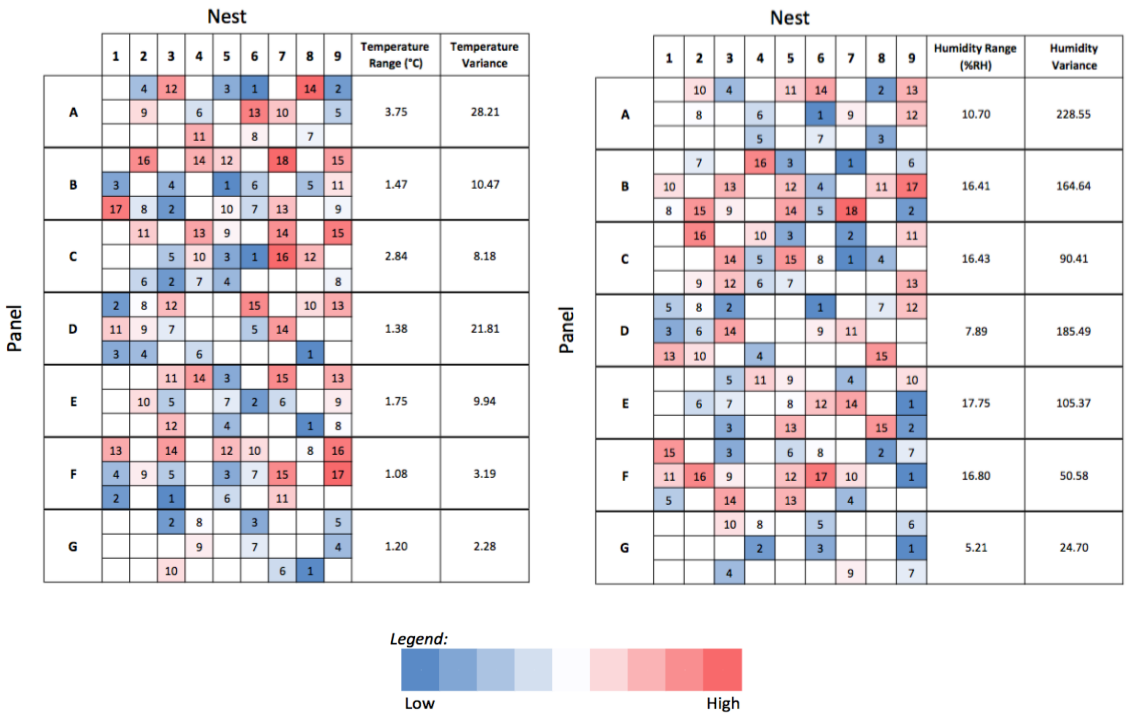


Figure 7. Variation in temperature (left) and humidity (right) between nest sites during sunny/warm day microclimate mapping. Both temperature and humidity represented via ranked values from low readings to high readings for measurements within each panel. Spatial mapping of ranked microclimate readings reveals no strong patterns in distribution of ranked temperature and humidity.

		Temperature			Humidity			
	All nests within each panel	DF, Error	F Ratio	Prob > F	All nests within each panel	DF, Error	F Ratio	Prob > F
Sunny/Warm Day	Panel A	13, 872	2.6516	**0.0012***	Panel A	13, 872	2.6334	**0.0013***
	Panel B	17, 1347	0.7771	0.7214	Panel B	17, 1347	5.3999	**< 0.0001***
	Panel C	15, 1051	5.3862	**< 0.0001***	Panel C	15, 1051	11.9334	**< 0.0001***
	Panel D	14, 683	0.3532	0.9862	Panel D	14, 683	0.9113	0.5462
	Panel E	14, 740	1.1928	0.2755	Panel E	14, 740	10.0830	**< 0.0001***
	Panel F	16, 841	1.6983	**0.0419***	Panel F	16, 841	16.6877	**< 0.0001***
	Panel G	9, 1126	6.8828	**< 0.0001***	Panel G	9, 1126	24.8705	**< 0.0001***
Cloudy/Cool Day	Panel A	13, 803	11.5784	**< 0.0001***	Panel A	13, 802	7.8183	**< 0.0001***
	Panel C	13, 417	21.0616	**< 0.0001***	Panel C	13, 417	9.9445	**< 0.0001***
	Panel D	15, 880	9.5848	**< 0.0001***	Panel D	15, 880	28.7519	**< 0.0001***
	Panel F	16, 767	1.6111	0.0602	Panel F	16, 767	4.1631	**< 0.0001***
	Panel G	12, 787	19.1266	**< 0.0001***	Panel G	12, 787	66.3409	**< 0.0001***

Table 6. Effect of nest site on microclimate within each panel during sunny/warm microclimate mapping days and cloudy/cool microclimate mapping days.

Cloudy/Cool Day Mapping

Panels A, C, D, F, and G were mapped on separate days that were qualitatively determined in the field to be cloudy, cool, and often somewhat rainy days at the study site. Some variation was observed between nests among all five panels (Figure 8), with one-way ANOVAs identifying a significant effect of nest site on both temperature and humidity within almost all panels (Table 6).

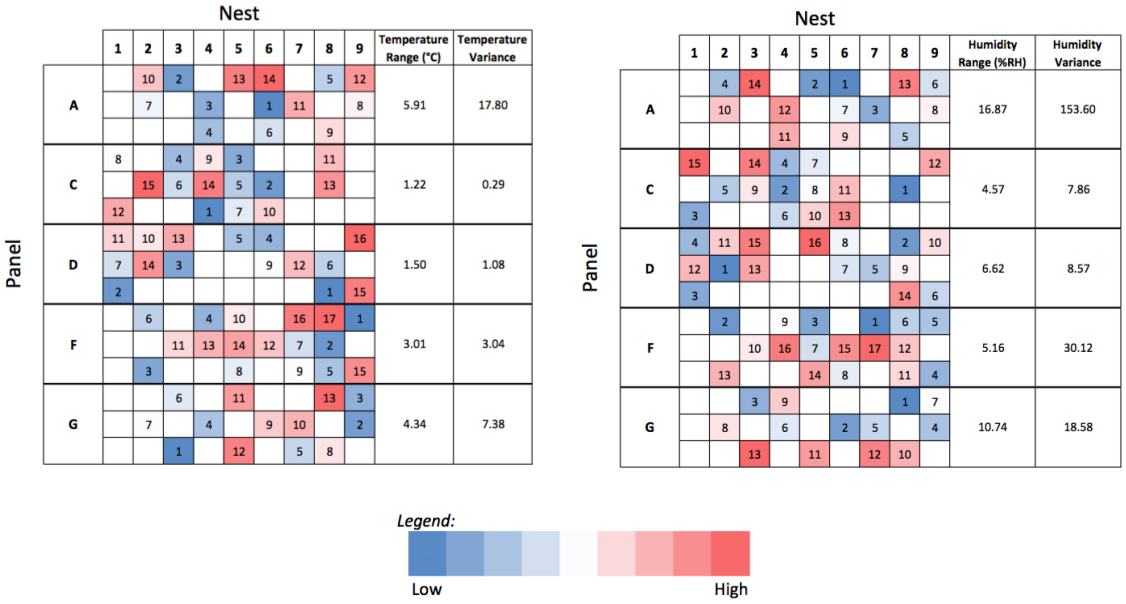


Figure 8. Variation in temperature (left) and humidity (right) between nest sites during cloudy/cool day microclimate mapping. Both temperature and humidity represented via ranked values from low readings to high readings for measurements within each panel.

Reproductive Parameters and Chick Growth and Development (2017 Season)

All reproductive parameters and chick growth and development data were collected during the 2017 field season only, with the exception of Q, which captures the reproductive success of nests on the tower as far back as the year 2000. The effect of microclimate on reproductive parameters and chick growth and development was

analyzed at both the coarser-level resolution of variation between panels (Tables 7 & 8) as well as the finer-level resolution of variation between individual nests (Tables 9 – 12).

Panel-Wide Analyses:

Julian Lay Date

Julian lay date was significantly affected by feeding condition ($F(1, 125) = 22.461$), $p < 0.0001$) and mean panel humidity ($F(1, 125) = 5.328$), $p = 0.023$), as determined via a one-way ANCOVA. Mean panel temperature had no significant impact on Julian lay date. Julian lay date was also significantly affected by both temperature variance ($F(1, 125) = 7.888$), $p = 0.006$) and humidity variance ($F(1, 125) = 5.576$), $p = 0.020$) across panels.

Clutch Size

Clutch size was significantly affected by feeding condition, which was determined via a one-way ANCOVA ($F(1, 125) = 28.722$, $p < 0.0001$). Clutch size was not significantly affected by mean panel temperature or humidity, nor was it affected by panel temperature and humidity variance.

Chick Body Condition Index (BCI)

A one-way ANCOVA determined chick BCI was significantly affected by feeding condition ($F(1, 65) = 9.040$, $p = 0.004$), however there was no significant effect of microclimatic means or variance between panels.

Proportion of Chicks Fledged (PCF)

There is a significant effect of feeding condition on PCF ($F(1, 76) = 10.215$, $p = 0.002$), with fed panels maintaining a higher PCF. There was no effect of mean panel temperature or humidity, nor any effect of panel temperature and humidity variances.

Table 7. Panel-wide analysis (ANCOVA) of the effect of mean microclimate and feeding condition on reproductive parameters and chick growth/development.

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Mean Temperature	1, 125	0.152	0.698
		Mean Humidity	1, 125	5.328	0.023*
		Feeding Condition	1, 125	22.461	< 0.0001*
	Clutch Size	Mean Temperature	1, 125	1.907	0.170
		Mean Humidity	1, 125	0.043	0.835
		Feeding Condition	1, 125	28.722	< 0.0001*
	Chick BCI	Mean Temperature	1, 65	0.106	0.746
		Mean Humidity	1, 65	0.163	0.688
		Feeding Condition	1, 65	3.529	0.065
Historic	PCF	Mean Temperature	1, 76	1.453	0.232
		Mean Humidity	1, 76	0.430	0.514
		Feeding Condition	1, 76	10.215	0.002*
	Q	Mean Temperature	1, 124	0.211	0.647
		Mean Humidity	1, 124	1.535	0.218
		Feeding Condition	1, 124	1.584	< 0.0001*

Table 8. Panel-wide analysis (ANCOVA) of the effect of microclimate variance and feeding condition on reproductive parameters and chick growth/development.

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Temperature Variance	1, 125	7.888	0.006*
		Humidity Variance	1, 125	5.576	0.020*
		Feeding Condition	1, 125	63.745	< 0.0001*
	Clutch Size	Temperature Variance	1, 125	1.742	0.189
		Humidity Variance	1, 125	0.151	0.698
		Feeding Condition	1, 125	54.218	< 0.0001*
	Chick BCI	Temperature Variance	1, 65	0.116	0.734
		Humidity Variance	1, 65	1.928	0.170
		Feeding Condition	1, 65	9.040	0.004*
	PCF	Temperature Variance	1, 76	3.297	0.073
		Humidity Variance	1, 76	1.546	0.218
		Feeding Condition	1, 76	16.849	< 0.0001*
Historic	Q	Temperature Variance	1, 124	0.783	0.378
		Humidity Variance	1, 124	3.893	0.051
		Feeding Condition	1, 124	40.065	< 0.0001*

Nest Site Analyses:

There was a slight effect of nest-site specific microclimate on Julian lay date, clutch size, chick BCI, and PCF.

Julian Lay Date

Julian lay date was significantly affected by mean sunny day nest temperature ($F(1, 69) = 6.193$, $p = 0.015$) and mean sunny day nest humidity ($F(1, 69) = 4.055$, $p = 0.048$), however it was not affected by nest variance in temperature or variance in humidity. Warmer and less humid nests tended to maintain earlier Julian lay dates.

Clutch Size

There was a trend toward a significant effect of mean sunny day nest temperature on clutch size ($F(1, 69) = 3.749$, $p = 0.057$), with warmer nests typically maintaining larger clutch sizes. Clutch size was not significantly affected by panel temperature and humidity variance during sunny or cloudy days.

Chick Body Condition Index (BCI)

Chick BCI was only affected by mean sunny day nest humidity ($F(1, 34) = 4.612$, $p = 0.039$), with chicks in more humid nests generally maintaining higher BCIs. There was no other effect of sunny day or cloudy day nest microclimatic means or variance.

Proportion of Chicks Fledged (PCF)

There was no effect of mean nest microclimate nor nest microclimate variance during both sunny days and cloudy days on PCF.

Table 9. Nest-site level analysis (ANCOVA) of the effect of sunny day mean nest microclimate on reproductive parameters and chick growth/development.

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Mean Temperature	1, 69	6.193	0.015*
		Mean Humidity	1, 69	4.055	0.048*
	Clutch Size	Mean Temperature	1, 69	3.749	0.057
		Mean Humidity	1, 69	0.194	0.661
	Chick BCI	Mean Temperature	1, 34	3.327	0.077
		Mean Humidity	1, 34	4.612	0.039*
	PCF	Mean Temperature	1, 42	0.284	0.597
		Mean Humidity	1, 42	0.056	0.814
Historic	Q	Mean Temperature	1, 69	2.133	0.149
		Mean Humidity	1, 69	0.606	0.439

Table 10. Nest-site level analysis (ANCOVA) of the effect of cloudy day mean nest microclimate on reproductive parameters and chick growth/development.

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Mean Temperature	1, 43	0.067	0.797
		Mean Humidity	1, 43	0.104	0.749
	Clutch Size	Mean Temperature	1, 43	0.148	0.702
		Mean Humidity	1, 43	0.208	0.650
	Chick BCI	Mean Temperature	1, 21	0.001	0.970
		Mean Humidity	1, 21	0.730	0.403
	PCF	Mean Temperature	1, 25	0.004	0.953
		Mean Humidity	1, 25	2.343	0.138
Historic	Q	Mean Temperature	1, 42	0.698	0.408
		Mean Humidity	1, 42	1.218	0.276

Table 11. Nest-site level analysis (ANCOVA) of the effect of sunny day nest microclimate variance on reproductive parameters and chick growth/development.

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Temperature Variance	1, 69	0.105	0.747
		Humidity Variance	1, 69	0.046	0.830
	Clutch Size	Temperature Variance	1, 69	0.132	0.718
		Humidity Variance	1, 69	0.387	0.536
	Chick BCI	Temperature Variance	1, 34	0.046	0.832
		Humidity Variance	1, 34	0.157	0.695
	PCF	Temperature Variance	1, 42	2.367	0.131
		Humidity Variance	1, 42	2.125	0.152
Historic	Q	Temperature Variance	1, 69	0.384	0.538
		Humidity Variance	1, 69	0.108	0.743

Table 12. Nest-site level analysis (ANCOVA) of the effect of cloudy day nest microclimate variance on reproductive parameters and chick growth/development.

Nest Site Analysis - Cloudy Day Microclimate Variance

	Model	Source	DF, Error	F Ratio	Prob > F
2017	Julian Lay Date	Temperature Variance	1, 43	0.173	0.680
		Humidity Variance	1, 43	0.092	0.763
	Clutch Size	Temperature Variance	1, 43	0.075	0.785
		Humidity Variance	1, 43	0.078	0.781
	Chick BCI	Temperature Variance	1, 21	0.345	0.563
		Humidity Variance	1, 21	0.804	0.380
	PCF	Temperature Variance	1, 25	0.104	0.750
		Humidity Variance	1, 25	0.401	0.533
Historic	Q	Temperature Variance	1, 42	3.071	0.087
		Humidity Variance	1, 42	2.678	0.109

Nest Site Quality (Historic: 2000 – 2017)

Nest site quality (Q) was significantly affected by feeding condition as determined by a one-way ANCOVA ($F(1, 124) = 1.584$, $p < 0.0001$), with fed panels maintaining higher Q. There was also a nearly significant effect of panel humidity variance on Q ($F(1, 124) = 3.893$, $p = 0.051$), with more variable panels maintaining slightly higher Q. However, there was no truly significant effect of microclimate means or variances on Q at the panel-wide or nest-site specific level (Tables 7 – 12).

In observing spatial trends of Q within panels, highest quality nests tend to cluster more towards the upper center of any given panel, with the bottom row of any panel often maintaining a majority of the lowest quality nests (Figure 9).

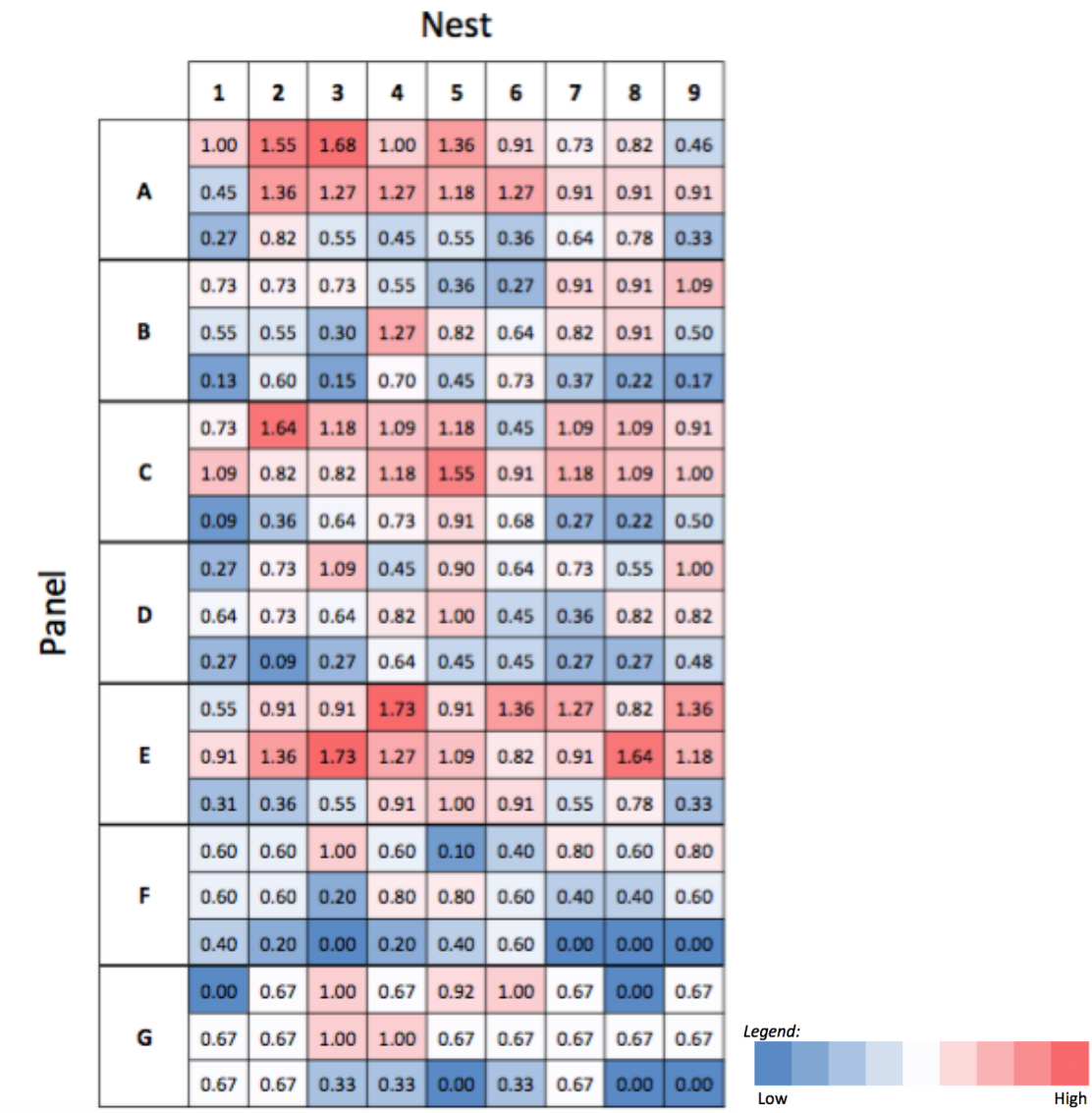


Figure 9. Nest site quality (Q) scores over 11 selected years between 2000 and 2017.

Temperature also follows a similar pattern in which the nests in the upper two rows tend to be somewhat warmer than those on the bottom row, as well as in humidity in which nests in the top row tend to be less humid than nests in the bottom row (Figures 7 & 8). This pattern is also reflective of the inverse relationship between temperature and humidity.

IV. DISCUSSION

I found that certain aspects of microclimate do contribute to variation not explained by food availability within a given breeding season. Warmer, less humid nests tended to be associated with earlier Julian lay dates and increased egg laying and Julian lay date was also affected by temperature and humidity variance at the panel-wide level. The fact that temperature does not impose a greater effect on developing chicks and breeding adults is surprising due to observations in the field of thermal impact on individuals, which materialized in clear demonstrations of behavioral thermoregulation among both chicks and adults. Behavioral thermoregulation was often seen in the form of gaping, or open-mouthed breathing or panting (Figure 10) (Buttemer and Astheimer 1990). Such behavior suggests that thermal strain may affect BLKI due to increased energetic expenditures. However, these data suggest that behavioral responses to high temperatures are effective, which results in little to no influence of nest site temperature on reproductive parameters of breeding adults or growth and development of chicks.

Figure 10. BLKI chicks and adults demonstrating gaping behavior during periods of direct insolation and thermal exposure at the nest. Photos supplied by ZMBF.

While microclimate does contribute to a small amount of variation in reproductive parameters, macroclimate still maintains a far greater impact on BLKI reproductive success as seen in the large effect of food availability (feeding condition) on reproductive parameters and chick growth and development. In light of our changing climate, this effect could indicate that BLKI will be far more sensitive to large-scale climate fluctuations, particularly in their impact on food availability. These fluctuations have become increasingly more dramatic as our climate changes, with a roughly 0.2°C increase in air temperature and 0.07°C increase in SST each decade—changes that are further emphasized by the PDO (IPCC 2007; EPA 2016; Mantua and Hare 2002).

Spatial Patterns of Microclimate

As predicted, there was significant variation in microclimate between panels A through G. Panel to panel variation was expected based on the fact that panels face

different directions, which results in differing exposures to the elements including rain, wind, and sunlight. Panel A faces southwest and panels B through F gradually transition from facing west toward north, ultimately reaching panel G which faces northeast. The roughly 240° exposure across all seven panels allows for a variety of microclimates to develop across these seven panels. Gradual changes in exposure to a variety of microclimatic variables across panels on the tower were reflected in patterns of higher mean temperatures and greater ranges of temperature exposure maintained on panels A, B, and C than the remaining panels D through G. These findings are consistent with field observations in which panels A, B, and C were often exposed to direct, intense, and often variable insolation and consequently higher nest temperatures during the warmest portions of the mid-day and afternoon period. Individuals within panels A through C were also most frequently seen gaping (behaviorally thermoregulating) primarily during times of most direct insolation.

By monitoring average panel microclimate through a majority of the egg laying and chick rearing period, I was able to characterize each panel's seasonal microclimate during a period crucial to breeding BLKIs' reproductive success. Since a BLKI's fitness is ultimately dependent on its reproductive success during the breeding season, it is important to quantify reproductive success and ultimately identify the variables that may be influencing its variability or stability and then relate those results back to the natural cliff-nesting setting of BLKI. Natural cliff faces also maintain highly variable directionality and exposure, and so variation due to nest positioning on the tower could

be reflective of variation experienced in nest sites distributed throughout the natural environment as well.

Microclimate Mapping

There was significant variation in microclimate between nests within each panel in both temperature and humidity measurements. Nearly all panels maintained significant variation in humidity measurements between nests within a given panel. Roughly three quarters of all panels maintained significant variation in temperature measurements between nests within a given panel. Heat map figures of each panel suggest that warmest nests tend to be found in the top two rows of each panel, however a consistent pattern was not evident (Figures 7 & 8).

The somewhat greater variation between nests in humidity than temperature could be due to a number of factors, including: 1. greater variation in direct nest exposure to rain, wind, and sunlight based on nest location (whether or not a nest is protected by any part of the tower structure), 2. nest shape, height, and building material (whether the nest is likely to retain more moisture and keep the nest site generally more humid), 3. the number of individuals that may be inhabiting that nest and therefore the amount of fecal matter that may accumulate on/around the nest, 4. nest site ventilation, 5. nest water-vapor conductance and the potential for egg water loss, and 6. any metabolic and respiratory activities of individuals at the nest site (Deeming 2011; Grant 1982). Small changes in temperature may often drive greater changes in humidity, which has been quantified in the natural environment with an increase in temperature leading to a greater decrease in humidity and vice versa (Chen et al. 1999). The factors listed above that may

be influencing humidity have the potential to vary dramatically between individual nests and are therefore more likely to influence humidity rather than temperature at the level of fine-scale variation between individual nest sites.

Reproductive Parameters and Chick Growth and Development (2017 Season)

Fed nests maintain earlier Julian lay dates. Julian lay date is also affected by microclimate, with earlier Julian lay dates found among generally warmer and less humid nests, suggesting that BLKI may adjust the timing of their breeding to short-term, small scale changes in climate such as the microclimate of their breeding site. However, Julian lay date was the only reproductive variable that clearly varied with microclimate. Most reproductive parameters only varied by feeding condition, further supporting the well-established fact that BLKI do adjust many of their breeding parameters to the larger-scale impacts of macroclimate, primarily SST, on food availability (Gill, Hatch, and Lanctot 2002). The adjustment of a reproductive parameter as a result of microclimate indicates BLKI's potential adaptability to localized microclimates and potential slight degree of resilience to large-scale climate change, being able to appropriately adjust the timing of egg laying accordingly to their breeding site microclimate (Frederiksen et al. 2014).

Analyses of clutch size indicated that, in general, larger clutch sizes are often associated with warmer nests. Ideal early stage incubation temperatures for BLKI are roughly 6°C to 11°C above ambient temperature, with BLKI eggs ranging in temperature from 11.9°C to 24.2°C six days or more after they are laid (Maunder and Threlfall 1972). As a result, increased nest temperature (higher than typical ambient temperatures of roughly 14°C) would be more favorable for incubating eggs. Therefore, higher nest

temperatures could be a potential indication to BLKI of a more optimal environment for egg laying and incubation because adults do not have to expend as much energy maintaining an increased nest temperature for successful egg incubation, ultimately leading to BLKI's response of increased clutch sizes in warmer nests.

Chick BCI was significantly affected by mean nest humidity, with higher nest humidity often associated with higher chick BCI. It is important to note, however, that the relationship between increased humidity and higher chick BCI may be the result of increased water weight of chicks in more humid nests affecting chick weight and ultimately impacting calculations of chick BCI by indicating chicks weigh more than their true mass when dry.

With the influence of chick water weight aside, however, the relationship between higher humidity and high chick BCI could be due to increased humidity providing a more optimal environment for chick development and thermoregulation, or perhaps it could be associated with differential survival of bacteria in the nest. If bacteria are in optimal humidity regimes then they will thrive, however if humidity regimes are above or below those required by certain bacterial strains, they could end up wiping out an entire bacterial colony (Dunklin and Puck 1948). Higher humidity could either function to prevent harmful bacterial exposure or provide an optimal environment for beneficial bacterial exposure and lead to increased chick BCI. Such phenomena have been explored in studies analyzing the effect of nest humidity on bacterial loads and ultimately on egg laying and reproductive success, which hypothesized higher nest humidity may be associated with earlier egg laying and increased reproductive success (Soler et al. 2015).

Though the present study found no effect of humidity on egg laying and reproductive success in magpies (*Pica pica*), that does not eliminate the possibility that humidity may affect microbial communities within BLKI nests and ultimately the chicks within them.

The nonsignificant effect of nest temperature on chick BCI conflicts with the results of Perez et al. (2008) in magpies in which increased temperature resulted in increased chick BCIs, however it does reflect results found in Konarzewski and Taylor (1989), which found no effect of air temperature on chick growth in little auk (*Alle alle*) chicks. The lack of effect of temperature on BLKI chicks may indicate their robustness to thermal stressors during growth and development or it could indicate the level of parental care received in order to shield chicks from these thermal stressors. Chicks' robustness to temperature may be essential to the survival of chicks of a cliff nesting species that would be heavily exposed to climate and weather on a cliff side from hatching through fledging. Temperature's lack of effect on BLKI chicks also indicates that any behavioral thermoregulation of chicks in response to thermal stressors and resulting energy expenditures are not large enough to significantly decrease energetic reserves available to invest in growth and development.

PCF was not affected by microclimate in any way, which is particularly interesting because it indicates that nest microclimate does not influence chicks' fledging success. These results indicate that adults are either relatively successful in their abilities to thermoregulate and maintain stable nest temperature and humidity needed for chicks during development, or chicks are capable of behaviorally thermoregulating successfully starting at a very young age.

Nest Site Quality (Q)

In the natural world, selection acts upon reproductive success, which ultimately determines fitness. Q is an important metric because it incorporates reproductive success over several years as opposed to PCF, which only analyzes the reproductive success of individuals at a nest site during the 2017 breeding season. Variation in microclimate or macroclimate within a single breeding season has the ability to affect reproductive parameters and chick BCI because they are all measures from within that one breeding season. However, Q characterizes average reproductive success of nest sites over time, therefore eliminating any year to year abnormalities and providing a more holistic representation of each nest site's reproductive quality.

Due to the fact that the tower is fixed in place, and relative sun exposure and prevailing wind patterns should not vary dramatically between years, I expected the relative microclimate of both nests and panels to remain the same over time. Therefore, by looking at reproductive success over several years, I could determine if the presumably consistent relative microclimate from 2017 predicts reproductive success over time.

Microclimate did not significantly affect Q, though there was a trend suggesting there may be an influence of panel wide humidity variance on Q, with generally more variable panels maintaining higher Q. The overall lack of significant effect of microclimate on Q ultimately indicates that microclimate may not explain much, if any, variation in reproductive success across breeding seasons.

Q is arguably the most informative variable quantifying the impacts of microclimate on reproductive success as a whole, rather than looking for effects in individual reproductive characteristics within a single year. The non-significant effect of microclimate on Q leads me to conclude that patterns in microclimate have not significantly affected reproductive success over the last decade or more, suggesting BLKI's overall reproductive success is robust to microclimatic variation.

These analyses have, in summary, determined that BLKI reproduction is responsive to certain aspects of microclimate. The warmest and driest nests are often the most favorable in the early stages of reproduction, with higher temperature and lower humidity often associated with earlier egg laying and increased clutch sizes. The fact that Julian lay date was affected by microclimate confirms that BLKI do have the ability to adjust certain reproductive parameters to their nest microclimate, suggesting BLKI are capable of sensing and adjusting to localized climates upon arrival. This concept was a point of concern in Frederiksen et al. (2004), which cautioned that if BLKI are unable to sense and adjust to the microclimate of their breeding site they may be even more highly susceptible to fluctuations in climate.

The lack of effect of microclimate on Q, however, most likely indicates that the range of microclimates found in nests on the Middleton Island tower simply does not have a strong effect on variation in reproductive success of nests over time. The robustness of BLKI to their microclimate could indicate an ability of BLKI to effectively compensate for thermal challenges behaviorally/energetically without compromising their reproductive and developmental abilities.

Role of Individual Quality

It is important to note that nest site selection and competition could lead to certain nests being more heavily selected for their more preferable microclimates, which would lead to increased competition and fighting over these nest sites, which was in fact observed in the field. Panel A, which was found to be a potentially more "optimal" panel for egg laying due to its slightly warmer temperature and lower humidity, was where a large portion of nest site competition and fighting was observed. Competition for nest sites would result in higher quality individuals already being more likely to win in competition and obtain these more optimal nest sites, which would then add the confound of individual quality to any effect of nest site microclimate on reproductive parameters.

In summary, microclimate could in fact be contributing to variation in reproductive success, or that variation could be due not to the influence of microclimate itself, but to the quality of the individuals that chose or were able to successfully compete for and win a nesting site with a more optimal microclimate. Competition for nest sites is more likely to result in higher quality individuals as winners and therefore inhabitants of these more optimal nesting sites. If these indirect impacts are occurring at Middleton, any increase in reproductive success may not be directly due to microclimate itself but to the quality of the individuals that were able to successfully inhabit those sites.

The confound of individual quality has proven to be incredibly difficult to tease apart in several studies, some of which have even demonstrated that nest microclimate may only influence reproductive parameters in conjunction with the influence of individual quality. Kim and Monaghan (2005b) have demonstrated that sites with more

optimal microclimates are often occupied by higher quality individuals, leaving it nearly impossible to eliminate the confound entirely. However, the results of the present study as well as those of Kim and Monaghan (2005b) still suggest that microclimate is an important factor in, at the very least, driving nest site selection by high quality individuals.

Other Potential Influences on Nest Microclimate

One other factor that could potentially be influencing variation in nest microclimate that has not been explored here is the influence of fed and unfed conditions on metabolism and consequently the effect of individual metabolism on the microclimate of the nest. In a brief qualitative analysis of patterns between panels, fed panels are found to be generally warmer in comparison to their unfed neighbors (Figure 11).

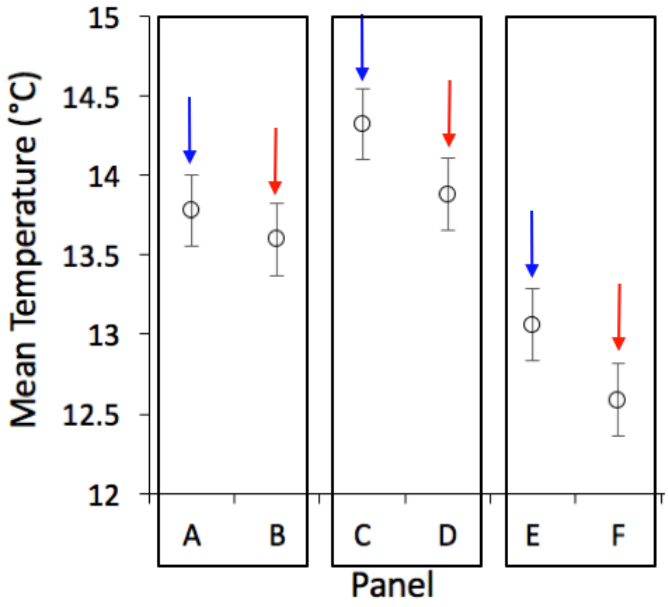


Figure 11. Mean panel temperature during the egg laying and chick rearing period. Blue arrows indicate fed panels, red arrows indicate unfed panels, rectangles partition qualitative pairwise comparison of neighboring panels

Fed birds will often remain at the nest following a supplemental feeding and therefore will metabolize at the nest, whereas unfed birds will be away from the nest actively foraging and metabolizing away from the nest site. Literature on avian metabolism has indicated that resting metabolic rate is affected by differing energetic demands (active foraging vs. ad libitum food supplementation), and therefore would be likely to maintain different thresholds between unfed birds who must actively forage for sustenance and fed birds who rely on food supplementation and therefore decrease their foraging bouts in both time and distance because of their readily available food source (Gabrielsen, Klaassen, and Mehlum 1992). Welcker, Speakman, Elliott, Hatch, and Kitaysky (2015) have also demonstrated that fed birds maintain higher average body temperatures than unfed birds. The difference in body temperature between fed and unfed birds, which could be further exacerbated by metabolizing at the nest, may influence nest microclimate. However, understanding this relationship is beyond the scope of the present study.

In summary, microclimate still only accounts for a very small portion of variation that is at times hard to separate from other potentially influential variables such as individual quality. Therefore, an increased sample size and further testing would be necessary in order to confirm these results. This study concludes, however, that certain aspects of microclimate do contribute to very small portions of variation not explained by food availability within a given breeding season, with warmer, drier nests tending to be associated with earlier egg laying and greater numbers of eggs laid, as well as greater mean humidity associated with greater chick growth and development. These results

therefore indicate that aspects of adult reproductive parameters as well as potentially of chick growth and development are affected, at least in part, by microclimate.

Despite the effects of microclimate on reproductive parameters and chick growth and development, feeding condition still maintains the strongest influence on variation in BLKI reproductive parameters and chick growth and development, indicating greatest sensitivity of BLKI to macroclimatic variation rather than microclimatic variation and ultimately confirming the validity of BLKI as a bioindicator species.

Though nest site humidity demonstrated some influence on chick growth and development, its effect was not particularly strong, which indicates a certain level of chick robustness to the effects of microclimate during early growth and development. Chicks' robustness to microclimate may be essential to their survival as a thermally exposed, cliff nesting species. The lack of effect of temperature is surprising due to prior observations of behavioral thermoregulation of both chicks and adults in response to thermal stress, however it again indicates the potential for great robustness of BLKI to microclimatic variability and strain.

BLKIs' sensitivity to feeding indicates that climate change on the scale of macroclimate will inevitably affect BLKI in terms of fluctuating SST and its effects on food availability. Other potential effects of microclimate may be eliminated via nest site selection, during which adults preemptively select nests with suitable microclimates and therefore do not expose themselves to the types of microclimatic extremes that would have the ability to impact BLKI reproduction.

Cam, Link, Cooch, Monnat, and Danchin (2002) write of the many potential variables influencing BKLI reproduction outside of climate, such as age and life-history traits. Though macroclimate is a very large contributor to variation in reproductive parameters and chick growth and microclimate is a much smaller, relatively non-influential contributor, there still exist many factors that could be influencing the kind of variation in reproductive success seen here between both nests and panels within a given year as well as between years. Ultimately, much is left to explore, however microclimate does contribute in small part to the variation we see in the reproductive success of breeding BLKI on Middleton Island, Alaska.

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